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ORIGINAL PAPER

The effects of thinning and gypsy moth defoliation on wood volume growth in oaks

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Abstract Stem dissection and dendroecological methods were used to examine the effects of thinning and defoliation by gypsy moth (*Lymantria dispar* L.) on wood volume increment in oaks (*Quercus rubra* L., *Q. alba* L., *Q. prinus* L.). A model was developed to evaluate radial volume increment growth at three time periods: before defoliation, during defoliation and after defoliation, as a function of species, defoliation intensity and crown position. Volume increment during these same time periods was also compared at different stem locations. Trees were defoliated for two consecutive years and results indicated that volume loss was greater during the second year of defoliation with complete recovery taking 2–3 years after defoliation. Oaks in thinned stands had similar reductions in annual volume increment during defoliation as those in the unthinned stand. Annual volume increment demonstrated a decreasing trend from stump to base of the live crown and volume increment of the lowest log (from stump height to 1.37 m), was always higher than upper log sections, even during defoliation. Both earlywood and latewood increments were reduced during defoliation; however, latewood reductions were distributed along entire stems while earlywood reductions were greater on upper stem sections within the crown.

Keywords Gypsy moth · Dendroecology · Oaks · Repeated measures analysis

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Introduction

The gypsy moth (*Lymantria dispar* L.) may be considered the most problematic defoliator of eastern deciduous forests. Feeding extensively on many species, the gypsy moth causes widespread decreases in growth and increases in mortality rates. The most preferred species include the oaks (*Quercus* spp.), aspen (*Populus* spp.) and basswood (*Tilia* spp.) (Montgomery et al. 1990; Twery 1987; Liebhold et al. 1995). For susceptible species, factors that influence the amount of growth decline or mortality include: the interaction of canopy position and tree vigor before defoliation; the intensity, duration and frequency of defoliation; and the presence of secondary-action organisms [e.g. *Armillaria* spp., *Agrilus bilineatus* (Weber)] (Wargo and Houston 1974; Dunbar and Stephens 1975; Campbell and Sloan 1977; Houston 1981; Parker 1981; Wargo 1981; Tigner 1992; Davidson et al. 2001). Trees of subdominant crown classes usually succumb first to gypsy moth defoliation, whereas dominant overstory trees can withstand several years of defoliation and survive (Campbell and Sloan 1977).

Effects of defoliation on stem form and growth

Trees not killed by defoliation typically have reduced apical and cambial growth. Even though height growth rate is generally not influenced by stand density (Oliver and Larson 1996), severe competition and defoliation can reduce foliar quantity beyond a critical threshold and suppress height growth (Mitchell 1975). In determinate species such as oaks, the number of leaves produced in the spring is largely preset in the previous year's buds, therefore shoot elongation usually ends early in the growing season (Kienholz 1941) and depends on reserves the tree has maintained over the winter (Kozlowski and Claussen 1966). Current year foliage is supported by the current year cambial growth layer primarily through the large vessels of the earlywood (EW) (Cochard and Tyree 1990). Hence, radial growth of the cambium starts before the leaves unfold (Zasada amd Zahner 1969). Northern red oak (*Q. rubra* L.) is considered a semideterminate species because all of the leaves in a growth flush expand and mature at about the same rate (Tomlinson et al. 1991). Current year latewood (LW) formation is strongly influenced by environmental conditions, such as precipitation and temperature during the current growing season (Fritts 1962). Current year defoliation negatively affected chestnut oak (*Q. prinus* L.) LW increment however, both current and previous year defoliation negatively effected LW increment in red and scarlet oaks (*Q. coccinea* Muenchh.) (Muzika and Liebhold 1999). Earlywood in many oak species tends to be less variable in width and less influenced by growing conditions than is LW (Rogers and Hinckley 1979; Phipps 1982; Woodcock 1989) because in the spring, developing foliage and EW are supported by photosynthates stored from the previous year. Therefore, declines in annual ring width from defoliation are largely the result of decreased LW formation (Varley and Gradwell 1968).

The vertical distribution of radial growth is not uniform over the length of the bole (Larson 1963; Duff and Nolan 1953) with a negligible amount slightly below the apex and the largest area increments at a point near the base of the crown and at the base of the stem (Pressler's Law as cited in Larson 1963; Assman 1970). Trees of a given height, diameter, age and species can have a different degree of stem taper because environmental conditions and stand density strongly affect stem form (Larson 1963; Mitchell 1975). The transverse and radial diameters of EW vessels in one annual ring of two stem-analyzed codominant red oaks, increased in direct proportion to the circumference of the main stem from top to base (Zasada and Zahner 1969). Reductions in stand density through thinning increases leaf area and stem sway in the wind. Subsequently, diameter increment increases, especially in the zone of butt-swell (Assman 1970; Waring et al. 1981; Smith et al. 1997).

Insect defoliations cause significant reductions in timber yield. Estimating the amount of volume production lost during an outbreak typically requires mathematical models and computer simulations (Valentine and Campbell 1975) because growth potential during the outbreak is unknown. Insect defoliations reduce foliage an indeterminate amount, therefore the effect of defoliation on cambial production is difficult to quantify. Most studies substitute radial or basal area growth at breast height (1.37 m above the ground) to measure the defoliation effect (Rose 1958; Kulman 1971; Stephens et al. 1972; Campbell and Sloan 1977; Wargo 1981; Muzika and Liebhold 1999; Naidoo and Lechowicz 2001). Twery (1987) used stem dissection to determine that during gypsy moth defoliation the lower bole of oaks lost a greater portion of its wood volume than did the upper portion, or stem as a whole. Thus any estimates of stem volume growth relying exclusively on samples from breast height (1.3 m above the ground) exaggerate volume growth increases during good years and growth reductions during poor years.

We used stem dissection and dendroecological techniques to determine the effects of thinning and gypsy moth defoliation on radial volume increment of red oak (*Q. rubra* L.), white oak (*Q. alba* L.), and chestnut oak (*Q. prinus* L.). All of these oak species have ring-porous wood with larger vessels produced in the EW transitioning to smaller vessels in the LW; the transition is generally more abrupt in white oaks (Panshin and De Zeeuw 1970). The purpose of the thinnings was to improve tree vigor in an attempt to minimize growth loss and mortality during defoliation. First, we developed a model to evaluate total stem volume increment growth at three time periods: before defoliation, during defoliation, and after defoliation, as a function of species, defoliation intensity and crown position. Then we compared total volume increment, and EW and LW volume increment, during these same time periods at different stem locations and for different thinning treatments.

Methods

Study area

The study area is located on privately owned forestland in Clinton County Pennsylvania near the town of Keating. In 1981, during the height of a gypsy moth defoliation event, a mixed-oak stand received intermediate silvicultural treatments to reduce tree susceptibility to gypsy moth defoliation by removing trees of low vigor. Three 160.9 × 181.0 m (2.9 ha) treatment areas (referred to as Stands 3, 4, 5) were established adjacent to each other on a southwest aspect. Nested within each treatment area was an 80.5 × 100.6 m (0.81 ha) measurement plot. Prior to treatment all trees >1.25 cm diameter at breast height (dbh, diameter at 1.37 m above ground) were numbered, tagged and tallied according to species, dbh and crown class (Smith et al. 1997).

Stand 4 received a low thinning that removed primarily overtopped, intermediate and weak codominant trees from the overstory canopy. Stand 3 received a similar treatment combined with a timber stand improvement operation to cut noncommercial-size stems between 5.0 and 11.5 cm. Stand basal areas were reduced 38 and 37% in stands 3 and 4, respectively. Stand 5 did not receive a treatment and served as the reference stand. The stands were defoliated by gypsy moth in 1981 and 1982. During the inventories associated with the outbreak years, tree crowns were visually evaluated and assigned to a defoliation severity class: Class 1 = 0–25% defoliation, Class 2 = 26–50%, Class 3 = 51–75% and Class 4 = 76–100%.

In 1987, 65 red, white and chestnut oak trees were randomly selected for destructive sampling from the 0.81 ha treatment blocks: Stand 3 = 22 trees, Stand 4 = 20 trees and Stand 5 = 23 trees. All trees were either dominant or codominant except for two intermediate crown class white oaks in stand 4. Because the treatment blocks are not replicated, each sample tree is considered an independent observation or replicate, nested within each treatment. The variance associated with each observation describes growth patterns associated only with this particular site. There were a total of 36 white oaks, 10 chestnut oaks, and 19 red oaks sampled. Due to the small sample of chestnut oaks, data for chestnut and white oaks were combined in the analyses and are hereafter referred to as white oak.

Prior to harvest, each stem received a paint mark at breast height on the north-facing side. Trees were felled at the base and stem cross sections cut at breast height, 1.37 m above breast height, and approximately every 1.2 m thereafter on the main stem. Sections were cut from both sides of forked stems. All sections were air-dried and sanded. Ring widths were measured to the nearest 0.001 mm along an average radius using a dissecting microscope in conjunction with J2X software (VoorTech Consulting 2000). The average radius was found by summing the diameter of the section in two perpendicular directions and dividing by four. Earlywood and LW were also qualitatively differentiated by vessel size, density and distribution, and measured on all rings along the average radius of each sample. The basis for distinguishing EW and LW was wood color and change in vessel size.

Analyses

The tree-ring series from the sample taken at 1.37 m was ring-dated using COFECHA software (Grissino-Mayer et al. 1997) and used as a master file for comparison with the rest of the disks from associated trees. Each ring series was then graphically cross-dated by matching pairs of narrow and wide rings with the master file. Two trees had low correlations of series segments with the master chronology (potential dating errors). However, inspection of the original samples showed the dating to be correct and none of the low correlations occurred for series containing years after 1950.

Because a stem cross section at stump height (0.1524 m above ground line) was not collected in the field, we used a method of Wiant and Williams (1987) to estimate stump diameter based on a known diameter at breast height:

$$D_s = \text{dbh} + B \times \text{dbh} \times \frac{2.557 - h}{h + 1}$$

where D_s = diameter (cm) at stump height during year n, B is a species-specific regression coefficient (0.20259 for red oak and 0.2121 for white oak), and h is stump height (0.1524 m). We estimated stump diameters for each year using the known dbh for the year of interest, and estimated total annual increment as well as annual EW and LW components.

Smalian's formula (Avery and Burkhart 1994) was used to calculate: (1) annual volume increment of EW by log, (2) annual volume increment of LW by log, and (3) total annual volume increment by log, which was then summed for the entire stem. Because of variability in tree heights and total number of log cross-sections, we calculated volumes according to log height relative to its distance from the stump and the base of the live crown with up to eight potential log sections:

V_S	Volume of stump log (stump to breast height)
V_1	Volume of log 1, 1.37 m section above breast height
V_2	Volume of log 2, section directly above L_1
V_3	Volume of log 3, section directly above L_2
V_{middle}	Volume of the log midway between the stump log and log located at the base of the live crown
$V_{amiddle}$	Volume of the log directly above the middle log
V_{top}	Volume of the log closest to the base of the live crown
V_{btop}	Volume of the log directly below VTOP

For trees with an even number of logs, we calculated the average of the two middle logs to estimate V_{middle} and $V_{amiddle}$. Logs were generally 1.2–1.37 m long, however, some logs were shorter (e.g. 0.6 m) or longer (1.8 m) due to branching and variations in total height. Therefore, volume calculations for all logs were standardized to 1.2 m using: relative volume = 1.2 × actual volume/actual length. We also calculated the volume increment ratio of annual volume increment of the stump log to the annual volume increment of logs at successive heights up the tree according to the following relationships: $V_{ratio1} = V_S/V_1$; $V_{ratio2} = V_S/V_2$; $V_{ratio3} = V_S/V_3$; $V_{ratio4} = V_S/V_{middle}$; $V_{ratio5} = V_S/V_{amiddle}$; $V_{ratio6} = V_S/V_{btop}$; $V_{ratio7} = V_S/V_{top}$. A similar procedure was used to compare EW and LW volume increment ratios. Sixteen trees, with less than eight logs, were not used in the ratio analyses.

The annual volume increments determined for each tree were then used in the construction of a polynomial model to estimate annual cumulative volume (m^3) increment as a function of dbh for each stand (Table 1). The annual dbh growth for years 1976–1980 (5 years pre-defoliation) was averaged for each stand and an average annual pre-defoliation growth rate was calculated. This constant rate was then used to annually increase dbh in the volume equation for the years 1981–1982 (during defoliation), and then for years 1983–1986 (post-defoliation) when diameter growth could have been either lower because of recovery from heavy defoliation, or higher because of crown release caused by mortality, thinning, or light defoliation. Even though studies of prolonged (10+ years) or repeated defoliation have shown negative effects on radial growth recovery (Naidoo and Lechowicz 2001), we assumed that trees would have grown on average at least at the rate they had been growing 5-years prior to defoliation because defoliation only occurred for 2 years. We then used the pre-defoliation polynomial equations to estimate what (stand) annual cumulative volume would have been for years 1981–1983 in the absence of defoliation, at the expected rate of diameter growth. The difference between the predicted and actual volume increment is the volume loss (Table 2). A similar procedure was used to predict annual cumulative volume loss by stand using the mean annual volume loss for the period 1981–1983; after 1984 actual growth exceeded predicted growth (Table 2).

General linear model analysis of variance (ANOVA) was used to compare the dependent variables "annual volume lost to defoliation" and "percent annual volume lost to defoliation" according to thinning treatment, species, defoliation year (1981, 1982, 1983) and the interaction of treatment × defoliation year. Because of unequal sample sizes among treatment areas, and species, multiple range tests used t tests of the least-squares means if the F statistic was significant. Least-squares means are the expected values of the means if the sample design was balanced. Duncan's multiple range test was used to compare annual volume loss for the three defoliation years (SAS Institute Inc. 2004).

Table 1 Coefficients for pre-defoliation polynomial models used to estimate annual cumulative volume (m^3) increment as a function of dbh

Stand (R^2 = 99.9)	#Trees	B_1	B_2	B_3
3	22	0.00566	–0.00511	0.00099585
4	20	0.00292	–0.00358	0.00089134
5	23	0.0183	–0.00542	0.00093870

Predicted annual cumulative volume = $B_1 + B_2 \times \text{DBH} + B_3 \times \text{DBH}^2$

We examined within-tree differences in mean annual volume increment and mean volume ratio by relative height for years 1975–1986 using repeated measures factorial analysis of variance. Relative log height was the repeated measures factor for both comparisons. We included treatment, species and time period (1975–1980 = pre-defoliation, 1981–1982 = defoliation, and 1983–1986 = post-defoliation) as additional main effects.

Repeated measures analysis of variance was used to compare mean annual volume increment, EW and LW volume increments, and the proportion of EW to LW volume increment (EW:LW) for three time periods (pre-defoliation, defoliation and post-defoliation) at up to eight locations on each stem. The sphericity assumption (homogeneity of covariance) was rejected and adjusted F values did not produce a satisfactory corrected epsilon (Greenhouse-Geisser) to modify a univariate test. A multivariate ANOVA was used for the analyses and harvest treatments (Stands 3, 4, 5) and species (red vs. white oaks) were viewed as separate, correlated dependent variables. Each level of mean volume (repeated factor called "height") was treated as a separate variable. Contrast analyses were used to compare volume increment of the butt log with the other seven stem/log locations. All statistical calculations were performed using Statistical Analysis Systems software (SAS Institute Inc. 2004).

Results

Predicted versus actual volume loss

Analysis of variance indicated that volume loss differed among stands, species, and defoliation year. Predicted annual volume increment (PAVI) was greater than actual annual volume increment (AAVI) ($P < 0.0020$) for the period 1981–1983 in all stands, with volume loss being greater in stand 4 compared to stands 3 and 5. Stand 4 had 14% greater ($P < 0.0001$) volume loss than stands 3 and 5 (Table 3).

The effect of defoliation year on volume loss and percent volume loss was also significant ($P < 0.0001$) and the multiple comparison tests indicated that volume loss during 1982 was significantly greater than 1981 (Table 3). By 1983 the loss had decreased to 0.00618 m^3, demonstrating some recovery from 2 years of defoliation. By 1984 AAVI was greater than PAVI only in stand 4 with growth recovery by 1985 in stands 3 and 5 (Table 2). Percent volume loss was significantly greater ($P < 0.001$) in white oaks (n = 46 trees) compared to red oaks (n = 19 trees) with 54% versus 40%, but actual volume loss did not differ. All trees were classified as >75% defoliated in 1981. By the following year, 16 trees remained in this

Table 2 The difference (volume loss = PAVI – AAVI) between predicted and actual annual volume increment was calculated for the period 1981–1986

Year	Stand 3				Stand 4			Stand 5	
	VL-BF	VL-m^3	%VL	VL-BF	VL-m^3	%VL	VL-BF	VL-m^3	%VL
1981	4.08	0.0096	54.98	2.67	0.0063	52.30	3.58	0.0084	47.58
1982	4.72	0.0111	61.85	3.11	0.0073	59.05	4.46	0.0105	57.91
1983	3.47	0.0082	45.47	1.95	0.0046	38.00	2.80	0.0066	35.94
1984	0.58	0.0014	10.11	–0.60	–0.0014	–4.69	0.13	0.0003	3.10
1985	–1.53	–0.0036	–14.70	–2.82	–0.0067	–41.10	–1.94	–0.0046	–21.49
1986	–3.31	–0.0078	–35.38	–4.37	–0.0103	–62.91	–2.97	–0.0070	–32.69

Annual percent volume change (%VL) [percent volume loss = (PAVI – AAVI)/(PAVI) × 100] was calculated for the same period. A negative value indicates that actual annual volume increment is greater than the amount predicted by the model. Volume loss (VL) is presented in units of board feet (BF) and cubic meters (m^3)

PAVI Predicted annual volume increment

AAVI Actual annual volume increment

Table 3 Least square means (standard error) of annual volume lost to defoliation and percent annual volume lost to defoliation for each defoliation year (1981–1982) and 1-year-post-defoliation

Defoliation year	#Trees	Volume loss[a] (m^3)	% Volume loss[b]
1981 (year 1)	65	0.00787 (0.00066)b	50.75 (3.93)b
1982 (year 2)	65	0.00942 (0.00068)a	59.75 (4.04)a
1983 (post)	65	0.00618 (0.00064)b	39.10 (3.93)b
Stand			
3	22	0.0068 (0.00041) b	42.40 (2.42)b
4	20	0.0088 (0.00040)a	55.92 (2.41)a
5	23	0.0079 (.00039)b	41.92 (2.32)b

Annual volume loss was also averaged for 1981–1983 and compared by thinning treatment. Values with the same letter (online) are not significantly different according to Duncan's multiple range test

PAVI Predicted annual volume increment

AAVI Actual annual volume increment

[a] Volume loss = PAVI – AAVI

[b] Percent volume loss = [(PAVI – AAVI)/(PAVI)] × 100

class and only six trees were classified as having 0–25% defoliation.

Annual volume increment comparisons

Significant differences were identified in mean total volume increment and mean volume increment of EW and LW according to treatment, species and defoliation period ($P < 0.0001$ unless otherwise indicated). Stand 4 had lower total volume increments ($P = 0.0057$) and EW increments ($P = 0.003$) than stands 3 and 5. Red oak total volume and EW volume increments were higher than white oak. Total volume increment, and EW ($P = 0.004$) and LW volume increments added during defoliation years were always lower than pre- and post-defoliation. The EW:LW ratio was always higher during defoliation.

The interaction effects of height × treatment, height × species, and height × period were significant for annual volume increment, EW volume increment ($P < 0.0006$, for height × period), and LW volume increment. Only the interaction of height × period was significant for the EW:LW ratio. The height effect (main effect of the repeated measures factor) was also significant for annual volume increment, EW volume increment, and LW volume increment because annual volume increment demonstrated a decreasing trend from stump height (V_S) to the base of the live crown (Figs. 1, 2, 3a–c). Annual volume increment, and EW and LW volume increments of VS were always significantly higher than all other volume increments at successive heights. Latewood volume increment decreased more than EW increment at successive heights hence the EW:LW ratio increased with height except during defoliation (Fig. 4).

Contrasts of stem volumes according to species were significant because red oak annual volume increments were always greater than white oak, regardless of stem location (Fig. 1c). Contrasts of defoliation period were also significant because increases in annual volume increment and EW and LW increment were always less for defoliation years. Contrasts of annual EW volume increment pre-, during and post-defoliation were significantly different between the butt log (V_S) and upper stem positions $V_{amiddle}$ ($P = 0.028$), V_{btop} ($P = 0.006$), and V_{top} ($P = 0.007$), but was not different from V_1, V_2, V_3 and V_{middle} (Fig. 2b). Alternatively, contrasts of the relationship of LW and total volume increment pre-, during and post- defoliation were significantly different between V_S and all other stem sections; even though V_S increment was reduced, it was still higher (Figs. 1b, 3b). However, the relative magnitude of the decrease in V_S increment was greater than the other stem sections (Fig. 5). Contrasts of EW:LW ratios pre-, during and post-defoliation were significantly different between the butt log (V_S) and upper stem positions V_{btop} ($P = 0.004$), V_{top} ($P = 0.006$), but were not different from V_1, V_2, V_3, V_{middle} and $V_{amiddle}$ (Fig. 4).

Stem location contrasts of total volume increment, and EW and LW volume increments according to thinning treatment were not significantly different. Therefore, even though stand 4 showed overall lower volumes than stands 3 and 5, the decreases in annual volume increment were similar among the three harvest treatments regardless of stem location.

Annual volume increment ratio comparisons

Annual volume increment ratio and LW volume increment ratios differed according to defoliation period ($P < 0.0001$ unless otherwise indicated) with the ratios during defoliation years always lower than pre-defoliation and post-defoliation, and post-defoliation always higher than pre-defoliation. (Figs. 1e, 3e). The treatment effect and species effect were not significant indicating that the increases in total and LW volume increment ratios were similar whether or not a stand had been thinned and similar for white and red oak. The EW volume increment ratio was only significant for species, with red oak having higher ratios than white oak (Fig. 2f).

The interaction effects of height × treatment, height × species, and height × period were all significant for annual volume increment ratio, LW ratios, and EW ratios ($P = 0.001$ for height × period). The height effect was also significant for annual volume increment ratio, and EW and LW volume increment ratios. Because there were smaller volume increments added at successive heights up the stem, mean annual volume increment ratio comparisons of stump sections to other sections increased with height (Figs. 1, 2, 3d–f). Contrast analyses were used to compare V_{ratio1} to the other six height ratios. Results indicated that the values of V_{ratio1} were always significantly lower than all other successive ratios because mean annual volume increment was more similar between the stump log/first log then between the stump log and successive logs up the

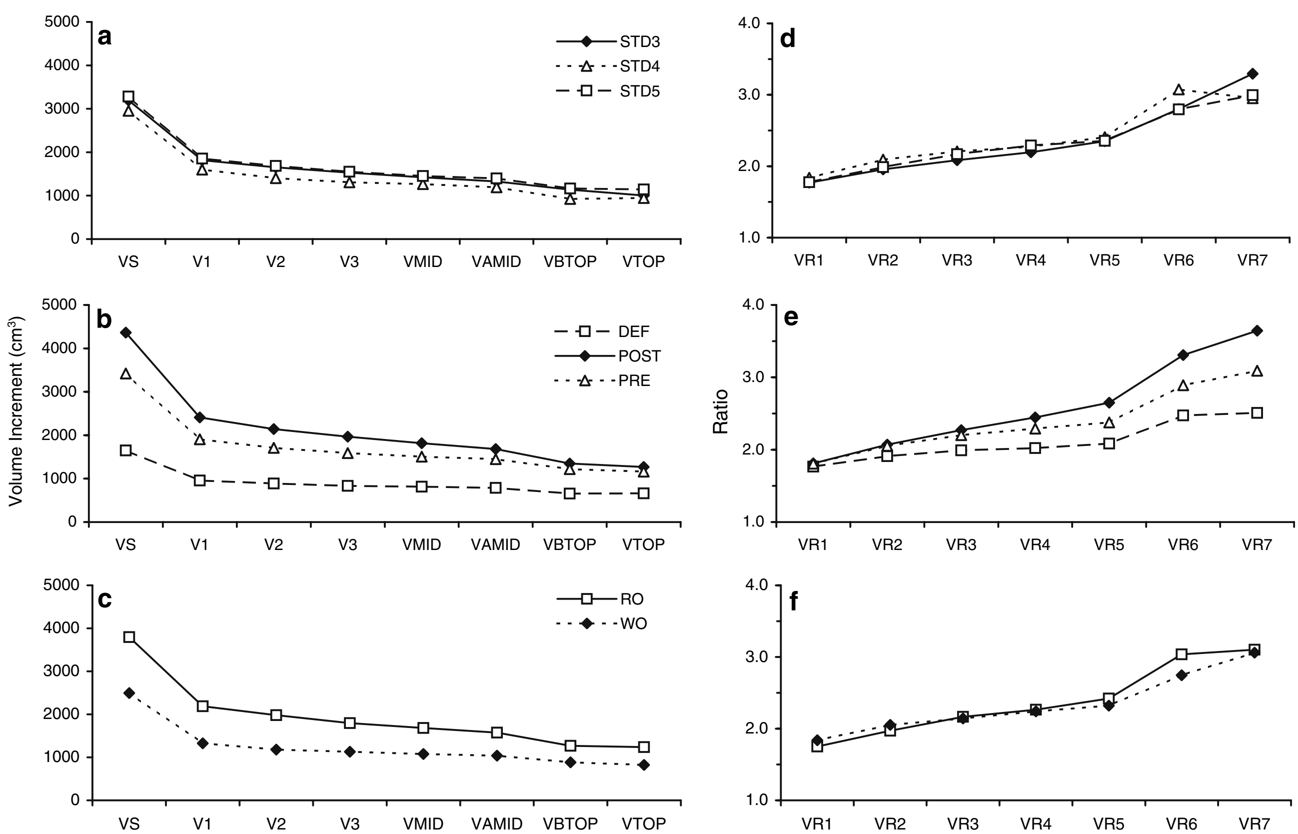

Fig. 1 Least square means of annual volume increment (Fig. 1a–c) according to log height relative to location above the stump. Least square means of annual volume increment ratios (Fig. 1d–f) of the bottom log to each of eight consecutive logs up the bole. Analyses were conducted according to treatment (Stand 3, Stand 4, Stand 5) (**a**, **d**), time period (*DEF* during defoliation, *POST* after defoliation, *PRE* before defoliation) (**b**, **e**), and species (*RO* red oak, *WO* white oak) (**c**, **f**)

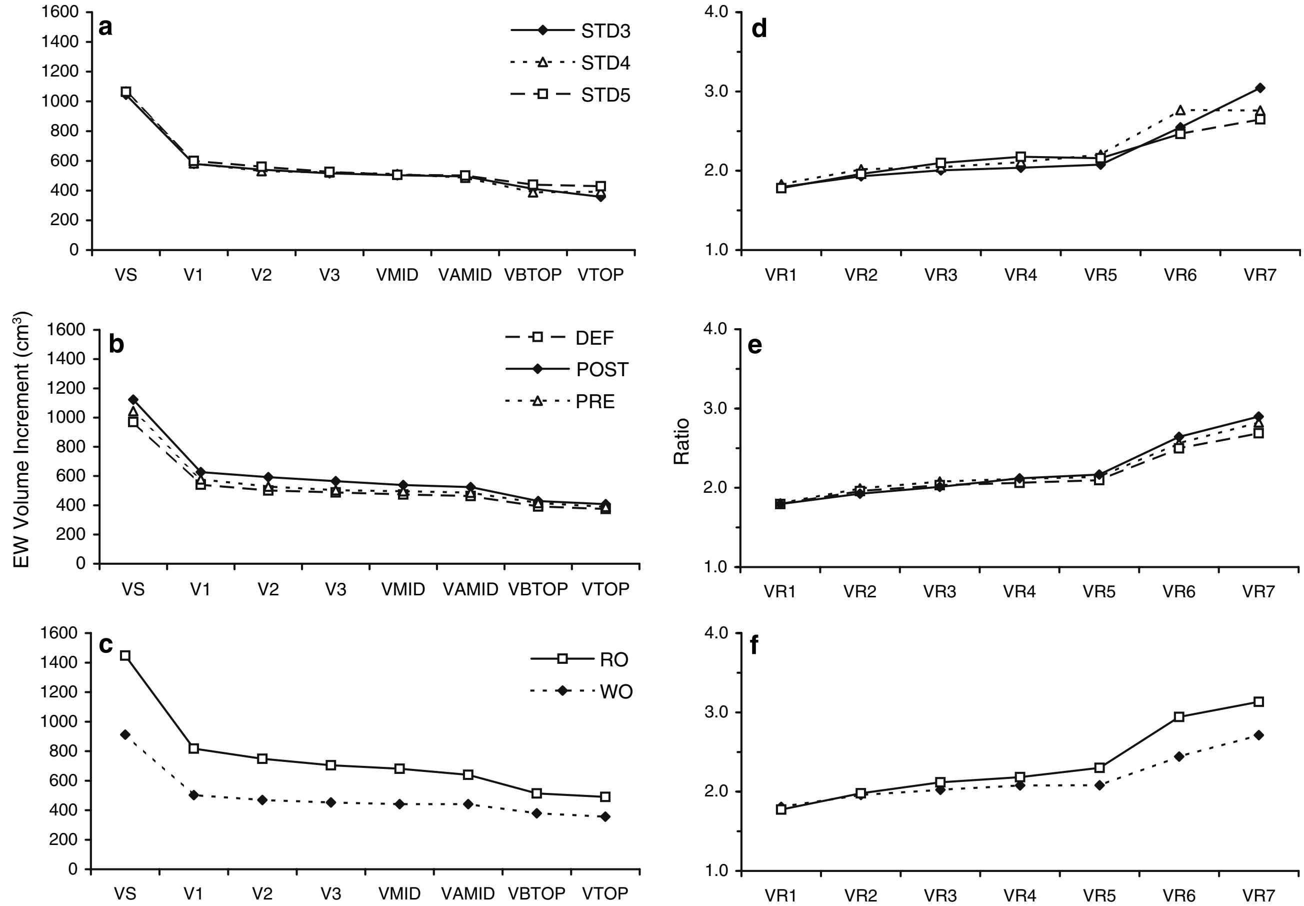

Fig. 2 Least square means of annual earlywood (*EW*) volume increment (Fig. 2a–c) according to log height relative to location above the stump. Least square means of annual EW volume increment ratios (Fig. 2d–f) of the bottom log to each of eight consecutive logs up the bole. Analyses were conducted according to treatment (Stand 3, Stand 4, Stand 5) (**a**, **d**), time period (*DEF* during defoliation, *POST* after defoliation, *PRE* before defoliation) (**b**, **e**), and species (*RO* red oak, *WO* white oak) (**c**, **f**)

stem. The height × treatment effect is only significant for annual volume increment ratio comparisons of V_{ratio1} to V_{ratio6} ($P = 0.016$) and V_{ratio7} ($P = 0.0007$) where stands 3 and 4 have higher ratios than stand 5 (Fig. 1d).

Contrasts of annual volume increment ratios were significantly greater for red oak than white oak when comparing V_{ratio1} to V_{ratio3} ($P = 0.003$), V_{ratio4} ($P = 0.005$), V_{ratio5} and V_{ratio6} (Fig. 1f). A similar species effect is significant for EW volume V_{ratio1} comparisons with V_{ratio3} ($P = 0.001$), V_{ratio4} ($P = 0.003$), V_{ratio5}, V_{ratio6} and V_{ratio7} (Fig. 2f) and LW V_{ratio1} comparisons with V_{ratio3} ($P = 0.008$) and V_{ratio6} ($P = 0.006$) (Fig. 3f).

All contrasts of ratios according to defoliation period were significant for annual volume increment (V_{ratio1} to V_{ratio2}, $P = 0.0019$) because even though all mean volume increments were severely reduced during defoliation years V_S increment was still higher than the rest of the stem (Fig. 1e). Similarly, contrasts of LW volume increment ratios were also significant (V_{ratio1} to V_{ratio3}, $P = 0.0097$) for defoliation years, except for V_{ratio2} (Fig. 3e). Earlywood volume increment ratios of V_{ratio1} to V_{ratio6} ($P = 0.006$), and V_{ratio7} were significantly higher during defoliation years than for EW ratios lower in the stem because upper stem sections added less EW increment during defoliation (Fig. 2e).

Discussion

Our estimates of predicted volume lost during defoliation years were more reliable than our predictions of post-defoliation volumes. Post-defoliation standard deviations of log section volumes from V_S to V_{amiddle} were 30–34% higher and top sections were 20% higher than pre-defoliation standard deviations. Therefore, post-defoliation volume increments were more variable than pre-defoliation indicating that individual tree health and growth recovery was not uniform and predictions of this time period were less reliable.

The second consecutive year of defoliation (1982) had significantly greater volume loss than the first year and

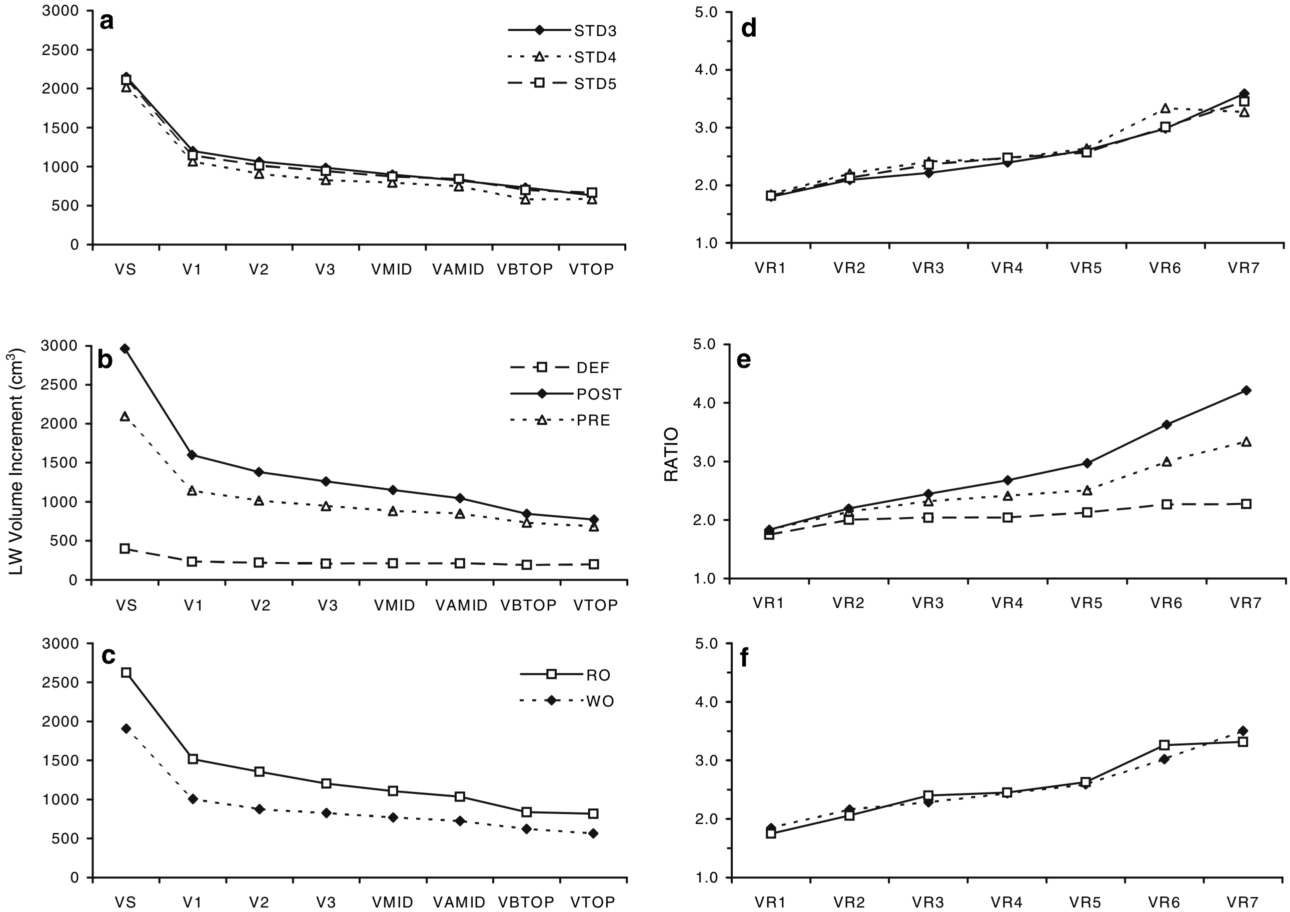

Fig. 3 Least square means of annual latewood (*LW*) volume increment (Fig. 3a–c) according to log height relative to location above the stump. Least square means of annual LW volume increment ratios (Fig. 3d–f) of the bottom log to each of eight consecutive logs up the bole. Analyses were conducted according to treatment (Stand 3, Stand 4, Stand 5) (**a**, **d**), time period (*DEF* during defoliation, *POST* after defoliation, *PRE* before defoliation) (**b**, **e**), and species (*RO* red oak, *WO* white oak) (**c**, **f**)

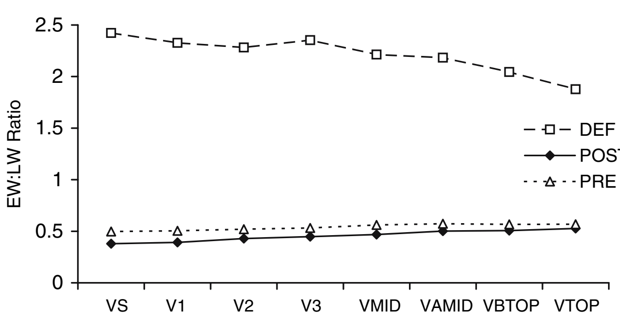

Fig. 4 Proportion of earlywood (*EW*) to latewood (*LW*) volume increment for three time periods (*DEF* during defoliation, *POST* after defoliation, *PRE* before defoliation) according to log height relative to location above the stump

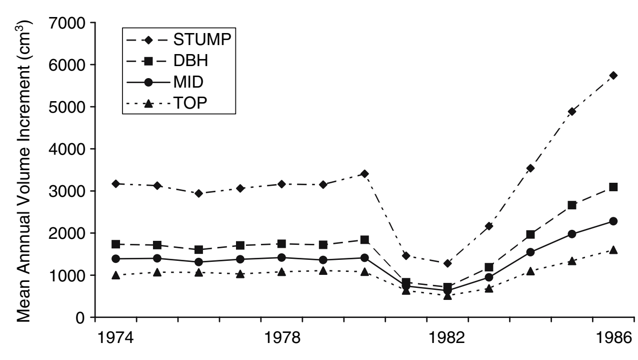

Fig. 5 Mean annual volume increments at four relative height locations on the bole: V_S stump to breast height (1.37 m); *DBH* 1.37 m section above breast height; *MID* log midway between stump log and log at base of live crown; *TOP* log closest to base of live crown. The *X*-axis indicates the years immediately before, during (1981–1982) and after gypsy moth defoliation

growth recovery to at least pre-defoliation levels took 2–4 years depending on the stand. Earlier studies have indicated that radial increment loss was proportional to defoliation intensity and duration. These studies also noted a lag effect with growth loss persisting the year following a defoliation event (Minott and Guild 1925; Baker 1941; Kucherov 1991; Huber 1993; Muzika and Liebhold 1999) but losses were evident for up to three years (Fratzian 1973; Magnoler and Cambini 1973; Twery 1987).

Our results did not indicate that thinning ameliorated the effects of defoliation on volume growth probably because the thinnings were conducted simultaneously with the first year of the outbreak. Residual trees did not have a chance to increase vigor in response to reduced stand densities. Volume loss during defoliation was greatest in stand 4 but regardless of defoliation, this stand always had lower annual volume increment, and EW and LW volume increments, compared to the other two stands (Figs. 1a, 2a, 3a). However, stand 4 showed positive growth recovery a year earlier than the other two stands. Stand 4 had the highest initial basal area prior to thinning (26.8 m^2/ha) versus stand 3 (23.8 m^2/ha) and stand 5 (24.8 m^2/ha) and the highest stocking at 114%. Stands 3 and 4 both had about 37% of their basal areas removed during thinning but stand 4 had almost 100 more residual trees per acre (235 vs. 139). From 1982–1985 stand 4 lost 3.8 m^2/ha to mortality while stand 3 lost 2.8 m^2/ha and stand 5 lost 5.1 m^2/ha. However, stand 4 had the highest percentage of trees die during this time period and 60% of this mortality occurred between 1982 and 1983. The higher mortality could explain the rapid growth increase of stand 4 to pre-defoliation volume increments and stocking levels a year sooner than the other stands.

Thinning resulted in greater annual volume increment on stump sections compared to upper stem sections, and regardless of thinning, red oak stump sections had greater increment ratios than white oak. Red oak diameter growth has shown a greater positive response to thinning than that observed for white oak, however, the difference was attributed to red oak's tendency to occupy dominant crown positions sooner (Graney 1987). Reducing stand density through thinning increases crown growing space (and other site resources) to residual trees and can cause a temporary acceleration of crown and stem increment before the tree returns to pre-thinning growth rate (Phipps and Whiton 1988). In a West Virginia study, released chestnut oak crowns had higher percent radial growth change than red oak but red oak's mean ring widths were still greater (Rentch et al. 2002).

Because our thinning treatments focused on removal of low vigor trees, those with smaller crowns and less stem taper, the trees sampled from the treated stands would have had larger crowns and better stem form (Larson 1963) before defoliation. In addition, the reduction in stem densities from thinning and defoliation-induced mortality produced more site resources for surviving trees to maintain their wood allocation priorities.

Our results also indicate that regardless of defoliation, the annual volume increment of the stump section was always higher than other stem sections. However, during defoliation the magnitude of the decrease for stump sections was much greater than for the other sections (Fig. 5). Even though our V_S values were based on stump diameter estimates, our results concur with other studies. Magnoler and Cambini (1973) found that defoliation resulted in greater reductions in radial increment in the crown than in the lower bole in cork oak (*Q. suber* L.). Twery (1987) also found that the annual volume increment of wood produced in the lowest log (0–2 m) was always higher than in the log at 5–10 m, even during defoliation periods. However, compared to average growth without defoliation, he noted that the lower bole (stump to breast height) lost a 5% greater portion of its growth during defoliation than did the upper stem. Physiologically, the upper bole shows a lesser decrease because there is an acropetal shift in wood distribution during years of low production; therefore growth does not decrease as much here during significant foliage reduction (Sundberg et al. 1993). During complete defoliation, ring porous species require only a small amount of hormonal stimulus from adventitious buds to trigger basipetal cambial activation (Wareing 1951). There is evidence that it is the metabolic activity of the cambium rather than the availability of carbohydrates that determines the allocation of wood production along the stem (Sundberg 1993; Uggla et al. 2001).

Effects of defoliation on wood properties

Seasonal activity of the cambium is regulated by hormones emanating from buds and expanding shoots. There is also evidence that concentration gradients of soluble sugars play a role as developmental regulators of pattern formation in cambial growth (Uggla et al. 2001). The first EW vessels of the current annual ring matures weeks before expansion of the first leaves (Zasada and Zahner 1969). An auxin precursor overwinters in the cambial region and its rapid conversion may be the reason for cambial initiation from the buds (Digby and Wareing 1966). There is strong evidence that the overwintering cambial region in red oak is preconditioned for the initiation of EW vessesls and that a signal from a relatively small number of buds is sufficient to initiate differentiation completely around the stem.

Because tracheid production is not directly related to indole-3-acetic acid (IAA) concentration in the cambial region, the initiation of latewood formation is not a consequence of decreased IAA concentrations in dividing and expanding cells. IAA probably has a role in defining the transition to cessation of cambial cell division associated with latewood formation (Uggla et al. 2001). Gypsy moth defoliation reduces leaf area and causes subsequent decreases in EW and LW production. During a severe defoliation, loss of leaves causes a tree to metabolize starch reserves, primarily in the roots. Oaks can deplete root starch reserves after at least 2 years of defoliation, depending on initial starch content and seasonal timing of defoliation (Wargo 1975a, b). Because EW production seasonally precedes gypsy moth defoliation, the reduced starch storage can lead to a reduction in EW production the following spring. Conversely, the effect of defoliation would be manifested in reduced LW production during both the year of defoliation and as a lag effect the following year. Hence, defoliation periods should show increases in the proportion of EW and loss in total increment (Huber 1982, 1993; Twery 1987; Asshoff et al. 1998–1999; Muzika and Liebhold 1999).

Our study indicated both EW and LW increment were reduced during defoliation but while LW was equally reduced along entire stems EW was more reduced on upper stem sections. The transition to LW cells first occurs at the base of the tree (farthest from the source in the crown) and moves acropetally (Larson 1964). Whereas, EW production continues longer into the growing season in upper stem sections, driven by diffusible auxin produced by the expanding shoots. Defoliation in early summer disrupts this latter auxin production and hence reduces EW production in the crown first.

For the period 1975–1986, total volume increment (Fig. 5), and EW and LW volume increment (Figs. 2a, 3a) of the stump, were always higher than for the rest of the stem. Defoliation caused the EW increment of the stump to be similar to everything below V_{amiddle}. Latewood, and hence total increment, was significantly reduced but the stump still had higher increment than the rest of the stem. The ratio of EW:LW was only significantly affected by defoliation and not by treatment or species, supporting the usefulness of this metric for reconstructing historic insect outbreaks in ring-porous species.

Under average growing condition, EW is characterized by large-diameter, thin-walled tracheids and LW is composed of narrow diameter tracheids with thicker cell walls. When the EW proportion is higher from defoliation, wood density (specific gravity) and strength are lower in ring-porous hardwoods because the LW vessels have more substantial (stiffer) cell walls (Schniewind 1959). Earlywood width is strongly associated with total vessel area so under favorable growing conditions EW is wider, and vessels and total vessel area tend to be larger. LW formation is under developmental, rather than metabolic control because it is the duration and not the rate of wall material deposition that causes the thicker tracheid cell walls (Skene 1972).

For example, the absence of water stress during the year of ring formation leads to the formation of more vessels and a thicker LW zone, resulting in a wider ring (Tardiff and Conciatori 2006). Alternatively, the first year after manual defoliation, EW vessels had smaller area in young *Q. robur* L. and *Q. patraea* Liebl. (Huber 1993). Tyloses can also form in EW during the defoliation year and the subsequent year probably because of stress in the water regime from reduced transpiration and decreased sapflow (Asshoff et al. 1998–99). Tyloses are an outgrowth of ray or axial parenchyma cells resulting from gas embolisms caused by loss of water in the vessels (Zimmerman and Brown 1974). Latewood width is more a function of the number of vessels indicating that LW vessels contribute little to total vessel area. Under tangential compression, yield strength is controlled by vessel collapse in the LW because these are probably supporting the larger vessels of the EW (Ljungdahl et al. 2006).

Our findings show that defoliation of oaks by gypsy moth reduced volume growth increment and wood strength properties more so in upper stem sections than in the lower bole. Because there was a lag effect on growth, EW:LW ratios were influenced for up to 5 years, inclusive of defoliation. Defoliation affected wood cellular properties, and the proportion of EW and LW because it alters the concentration and cambial distribution of sucrose, IAA, amino acid and nitrogen (Sundberg 1993). Oak lumber value for products, such as flooring and veneer, could be affected by the resulting weak zones created in the wood.

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